Setation and setal groups on antenna 1 of *Ridgewayia klausruetzleri*, *Pleuromamma xiphias*, and *Pseudocalanus elongatus* (Crustacea: Copepoda: Calanoida) during the copepodid phase of their development

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Abstract.—Setae added to the antenna 1 of three species of calanoid cope-pods during copepodid development are allocated to setal groups present on the adult antenna 1. Development of these setal groups is not homogeneous; for a given setal group the copepodid stage at which the first seta appears and at which setal addition is completed varies; whether the setal group is trithek or quadrithek in adult males also varies. These variations suggest several sets of setal groups as candidates for the presumed extra groups added during the adaption of an ancestral calanoid copepod to the pelagic environment. Among these, a set of late developing setal groups is preferred. A model for adding setal groups during copepodid development assumes three source groups are responsible for adding 16 progeny groups.

Antenna 1 of calanoid copepods usually consists of 25 articulating segments in adult females (Giesbrecht 1892) although 27 articulating segments have been found in some adult female epacteriscids (Fosshagen 1985). A calanoid antenna 1 with 27 articulating segments has been explained in one of two ways. The 27 segmented antenna 1 may be a state for calanoids which has been derived by fusion of the ultimate and penultimate segments from an ancestral copepod state with 28 segments (Huys & Boxshall 1991). Alternatively, it may be a state derived through the acquisition of extra segments, as the result of adaption by an ancestral calanoid to pelagic habitats, from an ancestral copepod state of about 20 segments (Stock 1991).

Here we examine these two hypotheses using data derived from the copepodid development of the calanoids *Ridgewayia klausruetzleri* Ferrari 1995, *Pleuromamma xiphias* (Giesbrecht 1889) [=*Pl. xiphias*] and *Pseudocalanus elongatus* (Boeck 1865)

[*Ps. elongatus*]. We analyze setation patterns of antenna 1 during development of these three calanoids. We allocate each seta at each copepodid stage to a setal group to which the seta will be associated in the adult female antenna 1, and derive developmental patterns for each setal group. We also discuss whether a homogeneous pattern of setation is present from which all of the setal groups in an ancestral 28-segmented appendage can be inferred, or whether several patterns are present among which is a pattern unique to a set of setal groups which can be identified as the extra, derived setal groups of calanoids. Finally we present a model for the addition of setal groups to antenna 1 during copepodid development of the three calanoids.

Methods

Ferrari (1995) described antenna 1 during the copepodid phase of development of *R. klausruetzleri*; Ferrari (1985) described the

development of copepodid (C) II–VI of *Pl. xiphias*; and Oberg (1906) described antenna 1 for CI-IV of *Ps. elongatus*. Here we add descriptions of antenna 1 of CI of *Pl. xiphias* and of CV-VI of *Ps. elongatus*, and redescribe the morphology of all of the stages while comparing the three calanoids.

The setose edge of antenna 1 has been called anterior (the direction of antenna 1 is held in calanoids) (Hulsemann 1991) but we note that among the remaining copepod appendages, most setae are found on the ventral edge (in descriptive work usually noted as medial) of an endopod; a few setae are found dorsally (usually noted as lateral). If the distal segments of antenna 1 are endopodal then the anterior edge of antenna 1 is ventral in copepods. The trithek/quadrithek groupings of setae on antenna 1 (Giesbrecht 1892) refers to the following set of setae: in the adult female a pair of setae originate close together often immediately proximal to an arthrodial membrane; one is a simple seta and the second, usually a modified, poorly sclerotized seta often is called an aesthetasc. A third simple seta is located proximal to the pair. In the CVI male a fourth, poorly sclerotized seta or aesthetasc may be present near the location of the above-mentioned pair.

Phylogenetic relationships among the 269 calanoid genera have not been proposed. The 43 calanoid families are grouped into 11 superfamilies and phylogenetic relationships among eight or 10 of those superfamilies have been hypothesized respectively by Andronov (1974) and Park (1986). *Ridgewayia klausruetzleri* [Ridgewayiidae, three genera] belongs to the Pseudocyclopoidea [three families], one of the two presumed oldest superfamilies, along with Epacteriscoidea; *Pl. xiphias* [Metridinidae, three genera] belongs to the Arietelloidea [eight families], the next most derived superfamily and presumedly the oldest superfamily of pelagic calanoids; *Ps. elongatus* [Clausocalanidae, seven genera] belongs to the Clausocalanoidea [11 families] the youngest superfamily. The analyses of Andronov (1974) and Park (1985), which revealed these relationships, used some of the same characters but neither analysis included as a character the number of segments of antenna 1.

Results

At CI, antenna 1 of all three calanoids has ten articulated segments. The setation of *R. klausruetzleri* from the proximal segment is 3, 2, 1, 2, 0, 1, 1, 3, 2, 7 (Figs. 1A, 2E), and for *Pl. xiphias* and *Ps. elongatus* it is 3, 2, 1, 2, 0, 1, 1, 2, 2, 7 (Figs. 3A, 4D, 5A, G).

At CII, antenna 1 of *R. klausruetzleri* has 17 articulated segments with 1, 4, 0, 1, 0, 2, 0, 1, 0, 1, 2, 1, 1, 1, 3, 2, 7 setae (Figs. 1B, 2D). Antenna 1 of *Pl. xiphias* has 15 articulated segments with two poorly expressed arthrodial membranes within the third segment; there are 3, 4, 1, 2, 0, 1, 0, 1, 2, 1, 1, 2, 2, 2, 7 setae (Figs. 3B, 4E). Antenna 1 of *Ps. elongatus* has 16 articulated segments with one poorly expressed arthrodial membrane within the first segment; there are 5, 0, 1, 0, 2, 0, 1, 0, 1, 2, 1, 1, 2, 2, 2, 7 setae (Fig. 5B, H).

At CIII, antenna 1 of *R. klausruetzleri* has 24 articulated segments with 1, 2, 1, 2, 0, 1, 0, 2, 0, 1, 1, 1, 2, 1, 1, 1, 1, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 1C, 2C). Antenna 1 of *Pl. xiphias* has 20 articulated segments with two poorly expressed arthrodial membranes within the sixth segment; there are 5, 1, 2, 0, 1, 2, 1, 2, 2, 1, 1, 1, 1, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 3C, 4F). *Pseudocalanus elongatus* has 19 articulated segments with poorly expressed arthrodial membranes within the first, fifth, sixth and seventh segments; there are 6, 2, 0, 1, 2, 1, 2, 2, 1, 1, 1, 1, 2, 2, 2, 7 setae (Fig. 5C, I).

At CIV, antenna 1 of *R. klausruetzleri* has 25 articulated segments with 2, 3, 1, 2, 1, 2, 1, 1, 3, 1, 1, 3, 2, 2, 3, 2, 2, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 1D, 2C). Antenna 1 of *Pl. xiphias* has 23 articulated segments with two poorly expressed arthrodial mem-
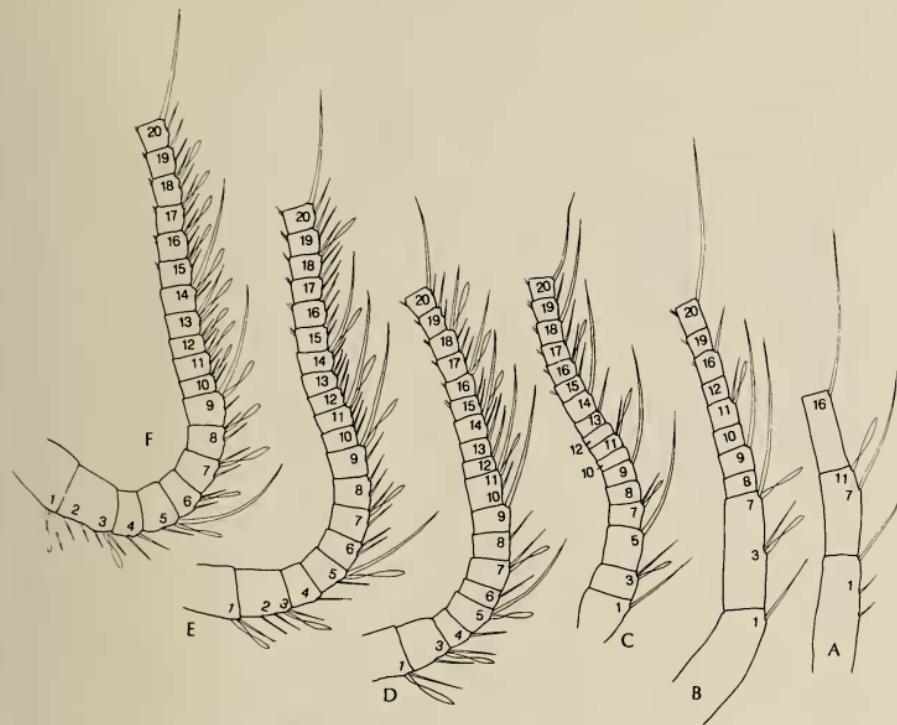
Fig. 1.   Proximal section of antenna 1 of *Ridgewayia klausruetzleri*. A, CI; B, CII; C, CIII; D, CIV; E, CV; F, CVI female. Illustrations not to scale; proximal is down; proximal section includes setal groups 1–20, if present; setal groups are numbered.

branes within the eighth segment; there are 7, 2, 1, 2, 2, 1, 1, 4, 1, 3, 2, 3, 2, 3, 2, 2, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 3D, 4F). Antenna 1 of *Ps. elongatus* has 22 articulated segments with two poorly expressed arthrodial membranes within the first segment and one poorly expressed arthrodial membrane within the fourth segment; there are 7, 2, 1, 3, 1, 3, 1, 1, 3, 1, 3, 1, 1, 1, 2, 2, 1, 1, 2, 2, 2, 7 setae (Fig. 5D, I).

At CV, antenna 1 of *R. klausruetzleri* has 26 articulated segments with 2, 4, 1, 3, 2, 3, 2, 3, 2, 3, 2, 2, 3, 2, 2, 2, 3, 2, 2, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 1E, 2C). Antenna 1 of *Pl. xiphias* has 23 articulated segments with two poorly expressed arthrodial membranes within the eighth segment; there are 9, 2, 3, 2, 3, 2, 3, 7, 3, 3, 3, 3, 3, 3, 3, 3,

3, 1, 1, 2, 3, 2, 7 setae (Figs. 3E, 4F). Antenna 1 of *Ps. elongatus* has 23 articulated segments with two poorly expressed arthrodial membranes within the first segment; there are 10, 3, 2, 3, 2, 2, 4, 1, 1, 3, 2, 3, 1, 1, 1, 2, 2, 1, 1, 2, 2, 2, 7 setae (not illustrated but see Fig. 5E, I).

At CVI, the female antenna 1 of *R. klausruetzleri* has 26 articulated segments with 2, 5, 2, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 2, 2, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 1F, 2C). Antenna 1 of *Pl. xiphias* has 22 articulated segments with three poorly expressed arthrodial membranes within the seventh segment; there are 10, 3, 3, 3, 3, 3, 12, 3, 3, 3, 3, 3, 3, 3, 3, 3, 1, 1, 2, 3, 2, 7 setae (Figs. 3F, 4F). Antenna 1 of *Ps. elongatus* has 24 articulated segments with one

Fig. 2.   Antenna 1 of *Ridgewayia klausruetzleri*. A, proximal section of CVI male; B, distal section of CVI male; C, distal section of CIII (distal section of CIV, CV, and CVI female is identical); D, distal section of CII; E, distal section of CI. Distal section includes setal groups 21–27; remaining explanation as for Fig 1.

poorly expressed arthrodial membrane within the second segment; there are 3, 7, 3, 2, 3, 2, 2, 4, 1, 1, 3, 2, 3, 1, 1, 1, 2, 2, 1, 1, 2, 2, 2, 7 setae (Fig. 5E, I).

At CVI, the right male antenna 1 of *R. klausruetzleri* has 24 segments with 2, 5, 2, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 2, 2, 5, 2, 3, 2, 7 setae (Fig. 2A, B); there is a geniculation between the 19th and the 20th segments. The right male antenna 1 of *Pl. xiphias* has 15 segments with three poorly expressed arthrodial membranes in the sixth segment and one in the seventh segment; there are 12, 4, 3, 4, 3, 14, 10, 6, 3, 2, 3, 5, 5, 2, 7 setae (Fig. 4A, B); there is a geniculation between the 11th and the

12th segments. Segment 12 bears distally a segmental attenuation which appears similar to two stiff, poorly-articulated setae found proximally on the segment; there also is a stiff, poorly-articulated seta on segments 10 and 11 (Fig. 4C). The right male antenna 1 of *Ps. elongatus* has 19 segments with 12, 4, 3, 4, 3, 4, 11, 2, 3, 2, 2, 2, 3, 2, 2, 2, 2, 2, 7 setae (Fig. 5F); there is no articulation. Morphology of the left antenna 1 of the CVI male is identical to that of the CVI female for all three calanoids.

There is a posterior seta on each of the last four segments of all three species at all six copepodid stages.
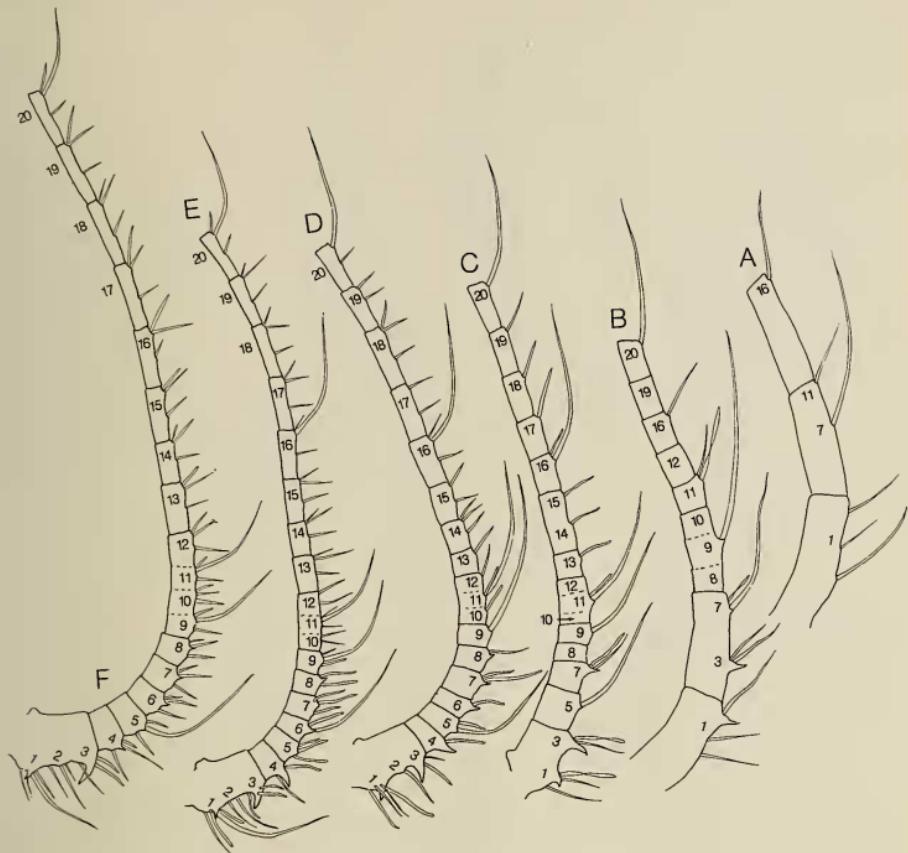
Fig. 3. Proximal section of antenna 1 of *Pleuromamma xiphias*. A, CI; B, CII; C, CIII; D, CIV; E, CV; F, CVI female. Dotted lines indicate incompletely formed arthrodial membranes; remaining explanation as for Fig 1.

Discussion

The presence of a proximal and a distal arthrodial membrane delimiting a group of setae traditionally has been used to identify the segments of antenna 1. Variation in expression of the arthrodial membranes, as described below, has led us to assign all setae present at each stage of development to one of 27 setal groups present in the adult female antenna 1 (Tables 1–3) without regard to the presence of arthrodial membranes. Assignment of setae during copepodid development to a setal group is based on the following four assumptions: during

development, setae usually are conserved (an exception is the loss of a seta by setal group 1 of *R. klausruetzleri* during the molt to CII); new setal groups usually bear one seta (exceptions: *R. klausruetzleri* setal groups 1, 3, 21, 25, 26, 27; *Pl. xiphias* setal groups 1, 3, 21, 25, 26, 27; and *Ps. elongatus* setal groups 1, 21, 25, 26, 27); arthrodial membranes may establish the location of a setal group before the first seta of that group is formed (setal groups 8, 10, 12, 19, 22 of all three species); and setae are added to a group so that the trithek/quadrithek groupings are conserved (a tri-

Fig. 4.   *Pleuromamma xiphias*. A, proximal section of right antenna 1 of CVI male (curved arrow unites setal group 6 with setal group 7); B, distal section of right antenna 1 of CVI male; C, detail of setal groups 19–23 on CV (to right) and CVI (to left) male right antenna 1 (long arrow near articulation of the proximal seta of setal group 20; arrowheads near poorly articulated setae of setal groups 19–21; open arrow near attenuation of segment bearing setal group 22); D, distal section of CI; E, distal section of CII; F, distal section of CIII (distal section of CIV, CV, and CVI female is identical). Explanations as for Fig 2.

thek/quadrithek grouping is not the out-
come for setal group 1).

Aside from truncations of setal addition
(Tables 1–3), developmental patterns of se-
tae generally agree among the three species.
The resulting adult female series aligns with
the 28-segmented adult antenna 1 presumed
for the ancestral copepod by Huys &
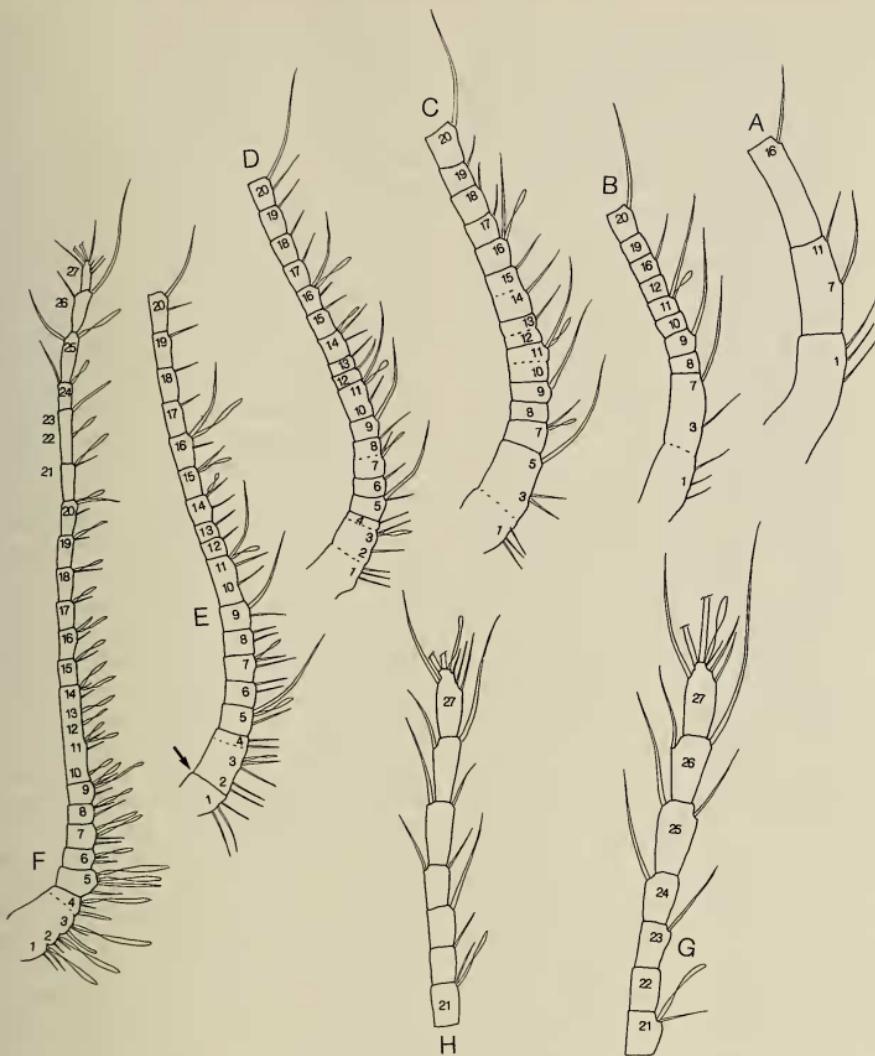
Fig. 5. Antenna 1 of *Pseudocalanus elongatus*. A, proximal section of CI; B, proximal section of CII; C, proximal section of CIII; D, proximal section of CIV; E, proximal section of CVI female (arrow indicates arthrodial membrane absent in CV; otherwise CV identical to CVI female); F, CVI male; G, distal section of CI; H, distal section of CII (distal section of CIII, CIV, CV, and CVI female is identical). Explanations as for Fig 2.

Boxshall (1991) with the exception of our distal setal group, which is represented by segments XXVII and XXVIII in the 28-segmented adult ancestor. As a result of this alignment, the geniculation on antenna 1 for the male of *R. klausruetzleri* and *Pl. xiphias*

occurs between homologous setal groups 20 and 21, as suggested for calanoids by Huys & Boxshall (1991) for their equivalent segments XX and XXI. However, our alignment does not match that suggested by Oberg (1906) for CI–CIV of *Ps. minutus*

Table 1.—For copepodids I–V, VI female (=f) and VI male (=m) [rows] of *Ridgewayia klausruetzleri*, setae are allocated to setal groups [columns]. Minus on the same side of contiguous numbers indicates that there is no or an incomplete arthrodial membrane between contiguous groups (e.g., between setal groups 7 and 11 in copepodid I).

Stage	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
I	3						-1				-1					1					2	0	1	1	3	2	7
II	1	-1	-2				-2	0	1	0	2	0	1			1	1		0	1	2	1	1	1	3	2	7
III		-2	2	1			2	0	1	0	2	0	1	1		2	2	1	1	2	3	1	1	2	3	2	7
IV	2		3	1	2	2	3	2	3	2	2	2	2	3	2	2	2	3	2	2	3	1	1	2	3	2	7
V	2	-2	-3	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2	3	1	1	2	3	2	7
VIf	2	-2	-3		3	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2	3	1	1	2	3	2	7
VIm	2	-2	-3		3	3	3	3	3	3	3	3	3	3	3	3	3	-3	2	2	-3	-1	-1	2	3	2	7

for which the four setae on the proximal section of CI are setal groups 9, 11, 16 and 20, and not setal groups 1, 7, 11 and 16 as proposed here (Table 3).

Incomplete arthrodial membranes vary among the stages of *Pl. xiphias* and *Ps. elongatus* studied here. However, in all cases the section of the arthrodial membrane that was present was much thinner than a complete arthrodial membrane, and the sector of the segment in which the arthrodial membrane was absent always included the anterior face. The above hypothesized setal allotments result in a complicated association of setal groups with arthrodial membranes. Early in development, arthrodial membranes are not expressed between setal groups that later in development become separated by arthrodial membranes; e.g., setal groups 7 and 11 at CI, and setal groups 3 and 7 at CII of all three species are not separated by an arthrodial membrane. Development of *Pl. xiphias* is more complicated. There is no arthrodial membrane between setal groups 3 and 7 at CII, but there is an arthrodial membrane between setal groups 1 and 3. At CIII the latter arthrodial membrane is not expressed, but a new arthrodial membrane is expressed between setal groups 3 and 7; thus setal group 3 becomes associated with setal group 1. Failure of arthrodial membrane expression is more common in adult males; e.g., compare adult male and female setal groups 3–4, 14–15, 16–17, 21–22, 22–23 and 24–25 of *Pl. xiphias*; setal groups 21–22 and 22–23 of *R. klausruetzleri*; or setal groups 3–4, 10–11, 11–12, 12–13, 13–14 and 22–23 of *Ps. elongatus*. Among the three calanoids, failure of arthrodial membrane expression proximal to one setal group coupled with a new membrane expression distal to the same setal group during immature copepodid development is found only in *Pl. xiphias*. However, this pattern may explain the phenomenon of setae that appear to jump across article boundaries at molts in other crustaceans (Grygier 1994).

Table 2.—For copepodids I–V, VI female (=f), and VI male (=m) [rows] of *Pleuromamma xiphias*, setae are allocated to setal groups [columns]. Minus on the same side of contiguous numbers indicates that there is no or an incomplete arthrodial membrane between contiguous groups (e.g., between setal groups 7 and 11 in copepodid 1).

Stage	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
I	3						-1				-1											0	1	1	2	2	7
II	3		-2				2	-0	1		2					1					2	1	1	2	2	2	7
III	-3		-2		1		2	0	1	-0	2	0				1	1		0	1	2	1	1	2	3	2	7
IV	-4			1	2		2			0	2	-0	1	1	1	2	2	1	1	1	3	1	1	2	3	2	7
V	-4	-1	-3	2	3	2	2	2	3	-1	3	1	3	3	2	3	3	3	2	2	3	1	1	2	3	2	7
VIf	-4	-3	-3	3	3	3	3	3	3	-3	3	-3	3	3	3	3	3	3	3	3	3	1	1	2	3	2	7
VIm	-4	-2	-3	-3	4	3	4	3	4	-3	-4	-3	4	-3	-3	-3	-3	3	2	3	-3	-1	-1	2-	-3	2	7

There is no evidence from the setal development patterns of these three calanoids for a homogenous pattern of setal development for all of the setal groups. The addition of the first seta to a setal group exhibits little variation; an exception is setal group 2 of *R. klausruetzleri* whose first seta appears at CV, rather than CIV as for the other two species (Table 4). However, not all setal groups begin with a single seta and not all setal groups add their second and third seta during contiguous molts. This lack of homogeneity may result from the addition of 16 setal groups during only five copepodid molts, unlike the thoracopods in which up to three setal groups are added during five copepodid molts. Alternatively these groups may not be homogeneous in their development because they are not evolutionarily equivalent; if the ancestral copepod possessed fewer than 27 setal groups, then different sets of setal groups may have been added to antenna 1 at different times during evolution to the calanoids.

Setal groups can be divided into several sets that differ in the number of setae present in each group of the adult male, or the initial condition of the setal group in its earliest copepodid stage, or the developmental pattern of the setal group. We will examine these sets for evidence of a set of setal groups that were added secondarily to the ancestral copepod state as an adaption to the pelagic environment.

There are no quadrithek setal groups on the male antenna 1 of *R. klausruetzleri*, perhaps because these animals spend part of each day in monospecific swarms (Fosshagen 1991, Ferrari 1995), where finding a female receptive to mating may not require searching a significant volume of water. If quadrithek setal groups are an adaption of calanoid males to search for receptive females in significant volumes of pelagic water, quadrithek setal groups may be the extra setal groups of calanoids. We do not consider the first setal group, which bears four setae in both adult males and females of *Pl. xiphias*, to be a true quadrithek. There are

Table 3.—For copepodids I–V, VI female (=f), and VI male (=m) [rows] of *Pseudocalanus elongatus*, setae are allocated to setal groups [columns]. Minus on the same side of contiguous numbers indicates that there is no or an incomplete arthrodial membrane between contiguous groups (e.g., between setal groups 7 and 11 in copepodid I).

Stage	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
I	3						−1			0	−1	0							0			0	1	−1		2	7
II	−3	−1	−1				−1	0	−1	0	2	−1							−1		2	1	1	2	2	2	7
III	−3	−2	−2	−1	−1		2	0	−1	0	−2	−1	1	1	1	−1			−1	−1	2	1	1	2	2	2	7
IV	−3	−2	−2	−2	2	−1	3	−1	−1	−1	3	−1	−1	3	−1	2	1	1	−1	−1	2	1	1	2	2	2	7
V	−3	−2	−3	−2	3	2	3	2	2	−1	−3	−1	−1	3	2	3	1	1	−1	2	2	1	1	2	2	2	7
VIf	3	−2	−3	−3	3	2	3	2	2	−1	−3	−1	−1	3	2	3	1	1	−1	2	2	1	1	2	2	2	7
VIm	−3	−2	−3		4	3	4	3	4	−1	−4	−1	−1	−4	2	3	2	2	2	3	2	−1	−1	2	2	2	7

five other setal groups (5, 7, 9, 11, 13) of the male of *Pl. xiphias* that bear four setae including a distinctive flask-shaped aesthetasc peculiar to the males. However, seven other setal groups (2–4, 6, 8, 10, 12) with only three setae also bear a distinctive, male-specific, flask-shaped aesthetasc. Males of *Ps. elongatus* also have five setal groups (5, 7, 9, 11, 14) of four setae, but seven other setal groups (4, 6, 8, 17–20) bearing one more aesthetasc than the female. Differing numbers of quadrithek setal groups and an apparent lack of serial homology of some setal groups bearing quadritheks, or distinctive or extra aesthetascs, suggests that setal groups with these identities are unlikely candidates for the set of extra setal groups of calanoids.

The initial condition of setal groups is variable but we can identify two sets: a set of five groups (8, 10, 12, 19, 22) whose location initially is established by the presence of a proximal and a distal arthrodial membrane before the first seta of that setal group appears; and a set of six setal groups (1, 3, 21, 25, 26, 27) that initially appear with more than one seta. Either of these setal groups are likely to be the extra set of the calanoids.

Setal development patterns also may be used to identify extra setal groups. In the case of adult females, there are setal groups that complete development late (those for which setation becomes complete at CVI or those for which the third seta of the trithek is added at CVI), and setal groups that begin development late (those for which the first seta appears at CIV) (Table 4). While the numbers of setal groups in each of these categories usually differ (Table 5, columns C–E), the setal groups, when present, are always homologous among the three species and are always found among the following set of setal groups: 2, 4, 6, 8, 10, and 12. We believe this set is the best candidate for the set of extra setal groups of calanoids, because development of these six setal groups is initiated and terminated late.

We hypothesize that some of the late de-

Table 4.—Copepodid stages (Arabic numerals) of *Ridgewayia klausruetzleri*, *Pleuromamma xiphias*, and *Pseudocalanus elongatus* at which the 1st, 2nd, and 3rd seta [rows] are added to a setal group [columns].

Seta	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
														Ridgewayia klausruetzleri													
1st	1	5	2	4	3	4	1	4	2	4	1	4	3	3	3	1	3	3	3	2	1	2	1	1	1	1	1
2nd	4	6	2	6	4	5	2	5	5	5	2	5	5	4	5	5	5	4	4	4	1			3	1		1
3rd			4		5	6	5	6	5	6	5	6	6	4	6	6	6	4			3						1
														Pleuromamma xiphias													
1st	1	4	2	4	3	4	1	4	2	4	1	4	3	3	3	1	3	3	3	2	1	2	1	2	1	1	1
2nd	1	5	4	5	4	5	4	5	5	5	2	5	5	4	4	3	4	4	4	4	1				1	1	1
3rd	1	6	5	6	5		5	6	5	6	5	6	5	4	5	4	5	4	5	5	2				4		1
														Pseudocalanus elongatus													
1st	1	4	2	4	3	4	1	4	2	4	1	4	3	3	3	1	3	3	3	2	1	2	1	2	1	1	1
2nd	1	5	3	5	4	5	2	5	5		2			4	5	3				4	1				1	1	1
3rd	1				5		5				5			4		4											1

Table 5.—Numbers of quadrithek setal groups of adult males (A); setal groups of the adult male with more setae than for the adult female (B); setal groups of the adult female in which the setation is completed at CVI (C); setal groups of the adult female with the third seta added at CVI (D); setal groups of the adult female in which the first seta appears at CIV (E).

	A	B	C	D	E
Ridgewayia klausruetzleri	0	0	10	8	5
Pleuromamma xiphias	5	7	6	6	6
Pseudocalanus elongatus	5	7	0	0	6

veloping setal groups are derived from the ectodermal cells of setal groups present during the early development of antenna 1. For the three calanoids studied here, we propose a model of development using five assumptions about which setal groups were likely source groups for later developing progeny groups: the number of source groups should be minimized; source groups usually should be present at CI; a source group may form more than one progeny group during the same molt; the location of a progeny group may be either proximal or distal to the source group; and a progeny group may be located between two arthrodial membranes before a seta appears. The first, third and fourth assumptions follow the segmentation model for harpacticoid copepods of Dahms (1989).

The model for these three calanoids (Fig. 6) includes three source groups (setal groups 3, 7, and 16). Two of them are present at CI (setal groups 7 and 16) and are not juxtaposed. At CI, 11 setal groups are present; group 22 lacks a seta. During the molt to CII, setal group 16 is the source of group 12 proximally and groups 19 and 20 distally; groups 12 and 19 each lack a seta. Setal group 7 is the source of group 3 proximally and groups 8–10 distally; group 3 possesses two setae at its formation and the distal groups 8 and 10 lack a seta. Group 22 has added its first seta. During the molt to CIII, setal group 16 is the source of groups 13–15 proximally and groups 17 and 18 distally; all have a seta and the first
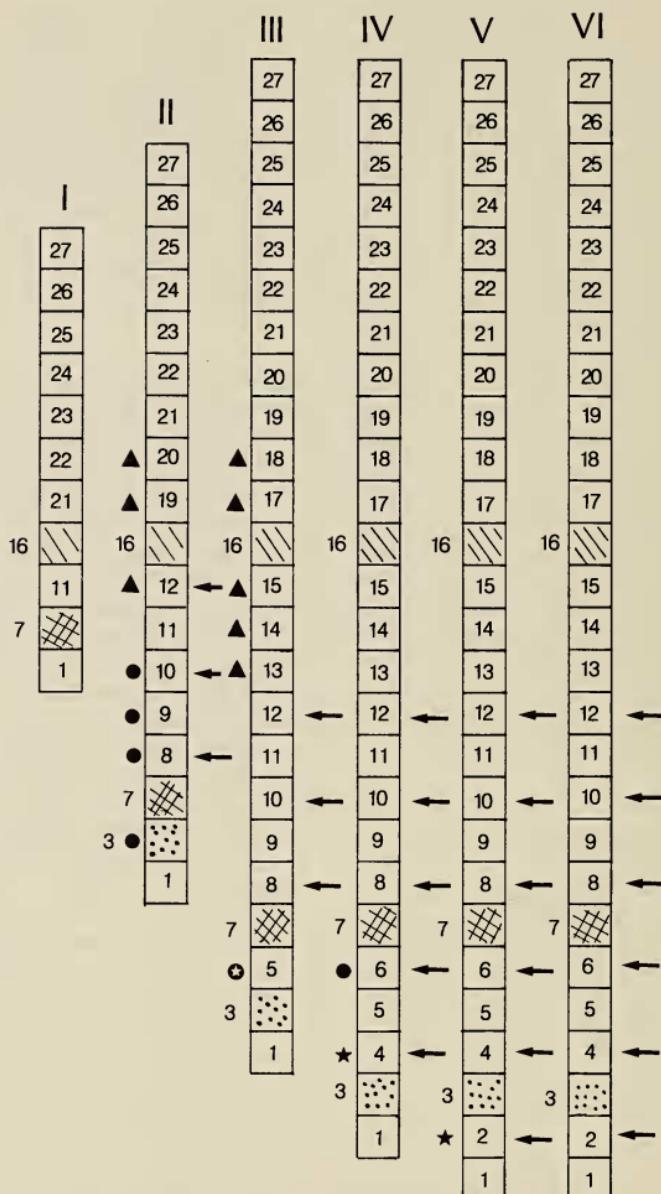
Fig. 6. Illustrated model of addition of setal groups to antenna 1 for CI–CVI (I–VI) of *Ridgewayia klausruetzleri*, *Pleuromamma xiphias*, and *Pseudocalanus elongatus*. Horizontal lines arbitrarily delimit setal groups (which are numbered) but do not necessarily indicate the location of arthrodial membranes; source group 16 is hatched; source group 7 is cross-hatched; source group 3 is stippled; triangles are to left of progeny of source group 16; circles are left of progeny of source group 7; stars are left of progeny of source group 3; setal group 5 (star in circle) may be a progeny of source group 7 or source group 3; arrows are to right of the preferred candidate set of extra, derived setal groups of calanoids, relative to an approximately 20-segmented state for the ancestral copepod.

seta of group 19 is added. Setal group 7 or setal group 3 may be the source of group 5, which has a seta. During the molt to CIV, setal group 16 is not active, but of its progeny, group 12 has added its first seta. Setal group 7 is the source of group 6, proximally, with its seta; of its earlier distal progeny, groups 8 and 10 each have added a first seta. During the molt to CV, setal group 3 is the source of setal group 2 proximally with its seta; setal group 3 is the only secondary source group formed from another source group (setal group 7).

Acknowledgments

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